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THE GENERA OF THE EBENALES IN THE SOUTHEASTERN UNITED STATES [1]

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OF THOSE COMPRISING THE EBENALES in the Englerian sequence of angiosperm families, four — Sapotaceae, Ebenaceae, Styracaceae, and Symplocaceae — occur in the southeastern United States, and it is these which are considered here as constituting the order. These four families, together with the Hoplestigmataceae, Diclidantheraceae, and Lissocarpaceae, also included by Engler and Gilg, are characterized by sympetalous corollas with stamens generally two or three times as many as the corolla lobes (or, by abortion, equal in number to and opposite them) and by superior to inferior, incompletely to completely loculed ovaries with axile placentation.

Wettstein, Engler and Gilg, Rendle, Cronquist, and Benson, among others, have retained the four larger families in a single order (although sometimes with additions), but others, as Hallier and Hutchinson, have split the group in various ways. Copeland (see Styracaceae) suggests that the order is a natural group with a collateral relationship to the Ericales and with an ancestry most nearly represented among living plants by the Theaceae. Altogether, the evidence from floral morphology and anatomy, pollen, wood structure, nodal anatomy, and embryology, insofar as this information is available, is in harmony with this view, and no very convincing data have yet been presented to the contrary. Various items in the

[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum made possible through the support of George R. Cooley and the National Science Foundation. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39:** 296–346. 1958). Other published portions of these studies will be found in Jour. Arnold Arb. **40:** 94–112, 161–171, 268–288, 369–384, 391–397, 413–419. 1959, and in the present issue. We are much indebted to the many people who have given freely of advice, information, or materials in connection with the four families treated here. In addition to our immediate colleagues, these include L. J. Brass, G. R. Cooley, W. H. Duncan, R. J. Eaton, R. K. Godfrey, Mrs. J. N. Henry, J. Kucyniak, J. D. Ray, Jr., H. W. Rickett, H. F. L. Rock, H. St. John, W. T. Stearn, F. A. Stafleu, and Mrs. C. E. Wood. The data on nodal anatomy are from the unpublished petiolar studies of R. A. Howard and are used with his kind permission. As in previous papers in this series, the illustrations are the work of Dorothy H. Marsh.

descriptions and discussions which follow will be found to bear on this problem.

At least some of the characteristics which often are cited in connection with the interrelationships of the families of the Ebenales need qualification and a great deal more investigation. For example, although the Sapotaceae are said to have completely septate ovaries, those of at least some (e.g., species of *Bumelia* and *Manilkara*) are at anthesis septate below but are no more completely so above than those of *Styrax*, and in inferior ovaries in both Styraceae and Symplocaceae a similarly incomplete condition occurs. Moreover, that inferior ovaries characterize five of the thirteen genera of the Styracaceae usually is glossed over in comparisons with the Symplocaceae. It should be remarked, too, that in the Ebenaceae, a single ovule in each locule seems to occur much more frequently than two, and there are indications that this condition may have come about through the development of additional septa which have separated the paired ovules. Indeed, all four families may well provide examples of increase in numbers of flower parts, rather than reduction. (Cf. the perianth and gynoecium of Sapotaceae and Ebenaceae and the androecium of Styracaceae and Symplocaceae, for example.) It is also noteworthy in connection with phylogeny that the ovules of Sapotaceae seem to have a single integument, those of Ebenaceae two, of Styracaceae either two or one (by fusion of the two), and of Symplocaceae one, although as yet very few representatives of these families have been examined.

SAPOTACEAE (SAPOTE FAMILY)

Armed or unarmed trees or shrubs with milky sap and alternate [rarely opposite], simple, exstipulate, usually entire and coriaceous leaves, the nodes with 3 traces from 3 leaf-gaps (except some species of *Bumelia*, 1 from 1). Inflorescences axillary, basically dichasial, ours simple, cymose or umbellate, or the flowers sometimes singly disposed, the pedicels bracteolate at the base. Flowers complete, regular. Calyx of 4–9[–12] imbricate, biseriate, or spirally arranged sepals, connate at the base. Corolla sympetalous, the lobes imbricate in the bud, usually as many as the sepals, sometimes with paired lateral or dorsal appendages. Stamens [twice as many as or] as many as and opposite the lobes of the corolla, epipetalous, distinct, the anthers 2-locular, longitudinally dehiscent; staminodia (when present) alternate with the fertile stamens and the lobes of the corolla. Gynoecium syncarpous, the style 1, the stigma unlobed or with as many lobes as locules, the ovary superior, the locules 1–14, typically 4 or 5, the placentation axile, a single, anatropous, 1-integumented ovule in each locule [except in *Diploön* with unilocular ovary and 2 ovules]. Fruit an indehiscent berry, often with a thin, leathery to bony outer layer; seeds large, with fleshy endosperm or none. TYPE GENUS: *Sapota* Mill. = *Manilkara* Adans.

A family of about 40 genera and more than 600 species, all woody, and primarily of the tropics of both hemispheres. Six of the approximately 15

genera of the Western Hemisphere are represented in the southeastern United States, but only *Bumelia* occurs outside of peninsular Florida in this area.

The Sapotaceae are distinguished from the other families of the Ebenales by the superior ovary which is usually completely septate (note illustration of *Bumelia*, however) and by the presence of a solitary ascending, 1-integumented ovule in each locule. The combination of laticiferous elements in leaves and stems and of two-armed hairs (one arm of which is sometimes suppressed) characterizes the family anatomically.

The delimitation of species and of genera, in particular, is difficult in the family, leading to both "splitting" and "lumping" at all taxonomic levels. After a period of neglect, a number of relatively recent studies have clarified the taxonomy and nomenclature of many groups, but it is likely that still further changes of both kinds will be made as the various groups become better understood. Taxonomic characters of generic significance have included especially the presence or absence of staminodia and endosperm, the presence or absence and location of appendages on the corolla lobes, and the general type of seed-scar (hilum).

Unfortunately, very few observations seem to have been made on the biology of the group, and little is known concerning the functioning of staminodia and petal appendages in connection with pollination.

The family is the source of a number of economically important timbers; the seeds of several genera provide edible oils; and a number of groups are valued for the refractive rubbery compounds from the coagulated latex (gutta-percha from species of *Palaquium*, *Payena*, and *Mimusops*; chicle from *Manilkara Zapota* and related plants; balata from *Manilkara bidentata* and related species). The family is also well known for a number of excellent tropical dessert fruits (most of which become quite rubbery and inedible when cooked), including the sapodilla (*Manilkara Zapota*), the sapote or marmalade plum (*Pouteria mammosa* (L.) Cronq., *Calocarpum Sapota* (Jacq.) Merr.), the eggfruit or canistel (*Pouteria campechiana*), and the star apple (*Chrysophyllum Cainito*).

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KEY TO THE GENERA OF SAPOTACEAE

A. Sepals imbricate or spiraled, not distinctly biseriate, 4–9, commonly 5, or sometimes in *Pouteria* decussate (2+2) when 4; flowers solitary in the axils or several to many in axillary clusters.
  B. Staminodia present, scale-like or petaloid, secondary lateral leaf-veins reticulate, not parallel to the primary ones; leaves glabrous or variously pubescent beneath (only in *Bumelia* sometimes rufous-sericeous).
    C. Flowers numerous in axillary clusters, small, the sepals 1–3.5 mm. long, the corolla 3–5 mm. long; hilum small, basilateral.
      D. Corolla-lobes without lateral lobes; ovary essentially glabrous; mature fruits 1.5–3 cm. long; endosperm present. ..... 1. *Mastichodendron.*
      D. Corolla-lobes with lateral lobes; ovary hairy or glabrous; mature fruits 6–12 mm. long.
        E. Plants unarmed; sepals pubescent; ovary glabrous (rarely slightly hairy); young and mature fruits commonly abruptly tapering into the style; endosperm present; cotyledons thin. ..... 2. *Dipholis.*
        E. Plants usually more or less spiny; sepals glabrous or pubescent; ovary usually hairy; young and mature fruits commonly broadly rounded to subtruncate or retuse at the apex; endosperm wanting; cotyledons fleshy. ..... 3. *Bumelia.*
    C. Flowers solitary or generally clustered in the axils, relatively large, the sepals 4–9 mm. long, the corolla 8–16 mm. long; hilum long, lateral; endosperm wanting; ovary hairy. ..... 5. *Pouteria.*
  B. Staminodia absent; secondary lateral leaf-veins (seen from lower surface after removal of trichomes) parallel to the primary ones; leaves densely rufous-sericeous beneath; flowers 4–7 mm. long; ovary hairy; endosperm present. ..... 4. *Chrysophyllum.*
A. Sepals in 2 distinct series, 6 (3+3), or occasionally 8 (4+4); flowers solitary or 2 or 3 together in the axils, relatively large, the sepals 4–10 mm. long, the corolla 4.5–13 mm. long; staminodia present, petaloid to fleshy, or sometimes nearly obsolete; hilum lateral; endosperm present. ..... 6. *Manilkara.*

Subfam. SIDEROXYLOIDEAE Lam

1. **Mastichodendron** Cronquist, Lloydia 9: 245. 1946.

Evergreen shrubs or trees with alternate or subopposite leaves, the midrib elevated on the lower leaf-surface, canaliculate above and often ending in a conical pouch at the summit of the long petiole, the blade pinnately open-reticulate veined, not closely areolate. Flowers numerous in axillary clusters. Sepals 5, suborbicular, spirally arranged. Corolla 5-lobed, firm-

textured, subrotate, the tube short, the lobes imbricate. Stamens 5, adnate to the corolla-lobes at or near the level of the sinuses; staminodia 5, not petaloid, shorter than the corolla-lobes. Ovary essentially glabrous, the locules usually 5, the ovules attached basilaterally. Fruit more or less fleshy, 1.5–3[–4.5] cm. long. Seed usually solitary, 1–2.5 cm. long, the hilum lanceolate to circular, to 9 mm. long, but not extending to the middle of the seed; embryo erect; endosperm abundant. (*Sideroxylon* sensu Dubard, Small, not L.) TYPE SPECIES: *Sideroxylon foetidissimum* Jacq. = *Mastichodendron foetidissimum* (Jacq.) Cronq. (The name from Greek, *mastico*, to chew, and *dendron*, tree, presumably alluding to chicle, the coagulated latex used as a base in the manufacture of chewing gum, obtained commercially from *Manilkara Zapota*.) — MASTIC, WILD-OLIVE.

As presently defined, a genus of about seven species of Florida, the West Indies, Mexico, and Central America; represented in our area by a single species in southern Florida.

Mastichodendron foetidissimum is an evergreen tree to 25 m. tall with long-petioled, yellow-green leaves with ovate to elliptic blades, glossy on both surfaces, the margins characteristically minutely puckered. The small, yellowish flowers appear throughout the year and are followed by one-seeded, juicy, yellow fruits 1.5–3 cm. long. The strong, dense, orange-colored heart-wood is sometimes used locally in cabinet-work and boat-building. Varietas *foetidissimum*, with broadly elliptic to suborbicular seed-scars mostly less than 4 mm. long, has a wide distribution from southern Florida through the West Indies from the Bahamas to Guadeloupe and Martinique. It occurs in the coastal hammocks of Florida as far north as Brevard County. Varietas *Gaumeri* (Pittier) Cronq., with larger, lanceolate or narrowly elliptic seed-scars, is known from British Honduras and Campeche and Yucatán, Mexico.

Dubard segregated the American species comprising *Mastichodendron* from the African *Sideroxylon* L. (type species, *S. inerme* L.) on the basis of the vertical (rather than horizontal) embryo and the open-reticulate (rather than closely areolate) venation of the leaf. However, he mistakenly applied *Sideroxylon* to the American species, treating the African as *Calvaria* Commers.; *Mastichodendron* is a renaming of the American group. *Mastichodendron* is considered by Cronquist to be the least specialized of the American genera.

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See family references, CRONQUIST (1946, Studies in the Sapotaceae — II, pp. 241–292), DUBARD (1912, p. 81), LAM (1939, p. 521), SARGENT (1893, pp. 161, 162, *pls. 241, 245*).

2. **Dipholis** A. de Candolle, Prodr. **8**: 188. 1844, nom. cons.

Unarmed shrubs or trees with pinnately veined leaves, the primary lateral veins not very numerous, sometimes obscure. Flowers of ours numerous in axillary clusters. Sepals (4–)5[–9], pubescent, obtuse. Corolla-lobes 5, rarely 6, obtuse, about as long as the tube, each lobe always with a pair of

acute lateral lobes or appendages at the base. Stamens as many as the corolla-lobes, the filaments adnate at or near the level of the sinuses. Staminodia petaloid, erose-fimbriate-laciniate, alternate with the lobes of the corolla and attached at or near the level of the sinuses. Ovary nearly always glabrous, rarely with short, appressed pubescence, 5-locular, the ovules attached basi-laterally. Fruit tapering abruptly into the short, persistent style, fleshy and to 1[–3] cm. long at maturity, black in ours, mostly 1-seeded. Seed with a very nearly basal [or rarely basilateral] hilum, the endosperm well developed, the cotyledons thin. (*Spondogona* Raf., 1836, nom. rejic.) TYPE SPECIES: *Dipholis salicifolia* (L.) A. DC. (The name from Greek, *di*, two, and *pholis*, scale, alluding to the paired corolla-lobe appendages.)

About 14 species, confined to tropical North America, with the principal concentration of species in the Greater Antilles (10 species), only one reaching southern Florida.

Dipholis salicifolia, bustic or cassada, of wide distribution, occurs in the hammocks of the Everglade Keys and the Florida Keys, in the Bahamas, southward through the West Indies to Guadeloupe and Barbados, and in southern Mexico, British Honduras, and Guatemala. It is a large shrub or tree (to 25 m.), evergreen, with elliptic to elliptic-lanceolate or -oblanceolate leaves, acute or acuminate at both ends. The numerous, small, white, fragrant flowers, borne more or less continuously throughout the year in simple, globose clusters at defoliated nodes or in leaf axils are followed by broadly ellipsoid or subglobose black fruits, 6–10 mm. long, containing one (or sometimes two or three) seeds. The very dense, red or dark-brown wood is sometimes used locally in cabinet work.

Similar to and perhaps derived from *Mastichodendron*, *Dipholis* differs from that genus primarily in the presence of lateral lobes on the corolla-segments. It is also closely related to *Bumelia* (see below).

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3. **Bumelia** Swartz, Prodr. Veg. Ind. Occ. 49. 1788, nom. cons.

Trees or shrubs, commonly but not always armed with spines or thorns, and with very tough wood. Leaves alternate or subopposite, generally small, the primary lateral veins not numerous, sometimes obscure, our species mostly with conspicuously reticulate-veiny leaves. Flowers 5(rarely 4 or 6)-merous throughout, 3-numerous in axillary clusters, proterogynous. Sepals glabrous or pubescent, oval or orbicular, obtuse. Corolla-lobes each with a pair of lateral lobes or appendages at the base [or these sometimes wanting]. Stamens epipetalous, opposite the corolla-lobes, the anthers extrorse, the filaments slender. Staminodia petaloid, entire, erose or laciniate, attached to the corolla alternate with the stamens at or near the level of the

sinuses. Ovary usually hairy, sometimes glabrous, the ovules usually 5, attached basilaterally. Fruit generally broadly rounded, subtruncate or retuse at the apex, 1-seeded, fleshy at maturity, purplish black, and not over about 1.5[–2.5] cm. in length. Seed with a small, nearly basal hilum, without endosperm, the cotyledons fleshy. (? *Robertia* Scop. 1777, nom. rejic.) TYPE SPECIES: *Bumelia retusa* Sw. (The name ancient Greek for a kind of ash-tree.) — BUCKTHORN, IRONWOOD.

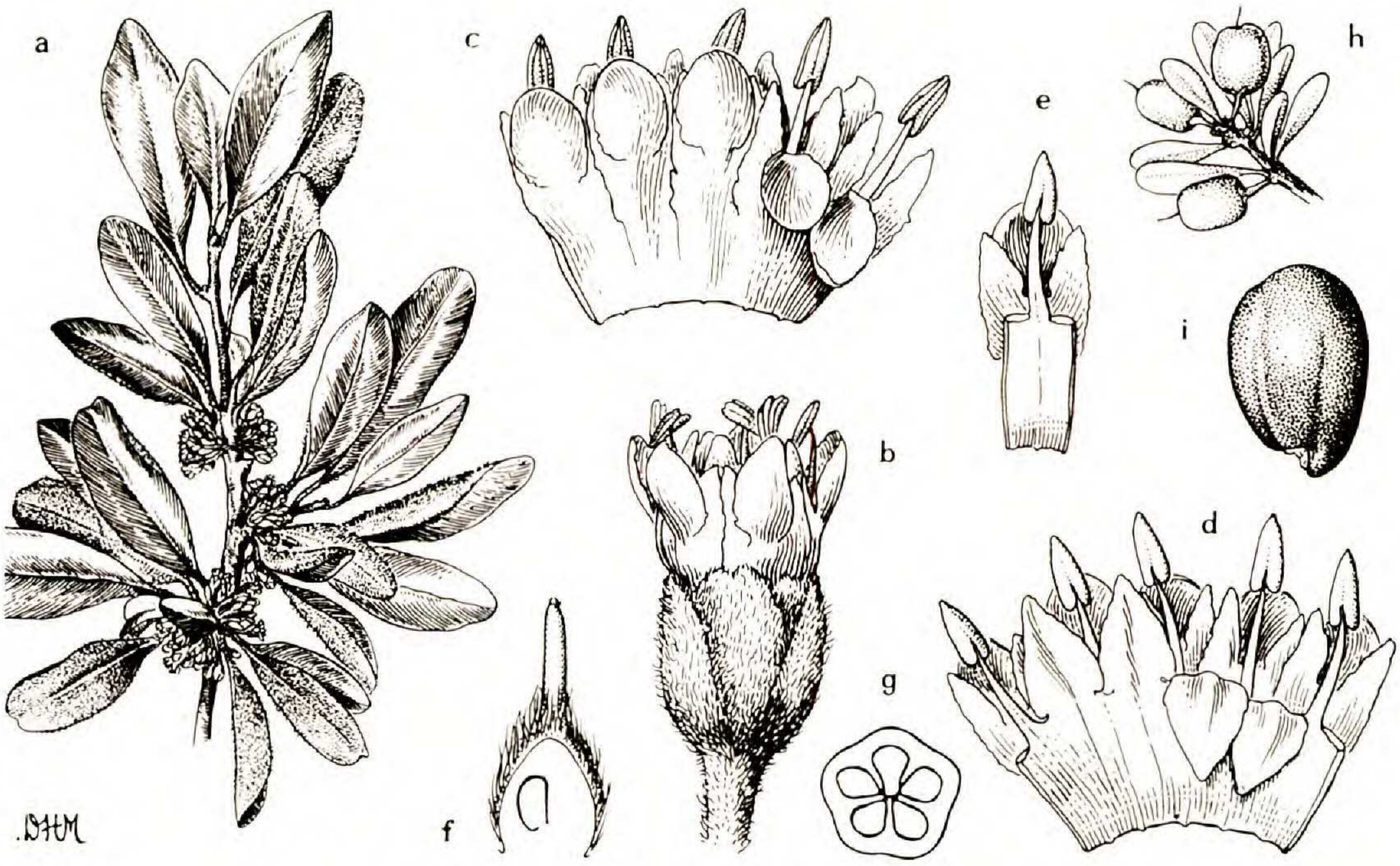

FIG. 1. **Bumelia.** a–g, *B. lanuginosa* subsp. *lanuginosa*: a, flowering branchlet, × ½; b, flower, × 6; c, opened corolla, from without, two petals turned down to show lateral appendages and stamens, × 6; d, opened corolla from within, two staminodia turned down to show lateral appendages of petals, one staminodium removed, anthers drawn as though erect (cf. b), × 6; e, single petal with appendages and stamen from within, × 6; f, gynoecium, with ovary in vertical section to show ovule, × 10; g, cross section of ovary above point of attachment of ovules to show five ovules and incomplete septation of ovary (semidiagrammatic), × 15. h, i, *B. celastrina*: h, tip of fruiting branchlet, × ½; i, seed, lateral view, × 2.

About 25 species, chiefly of the warm regions of North America, a few species in South America, reaching northern Argentina. The genus is well developed in both continental and Caribbean North America. About six species occur in our area.

A number of the species of *Bumelia* are widespread and variable. Specific lines are difficult to determine, and constant morphological characters are few in number. Pedicel-length, used in the past as a basis for specific distinctions, is extremely variable and unreliable. Form and color of pubescence are helpful in delimiting the entities, but considerable changes may accompany age, the young leaves and twigs being quite different in appearance from the mature ones. Clark recognized 12 species in the southeastern United States; Cronquist admitted only 6 from the same area, but

included essentially the same number of entities under a different hierarchical arrangement.

Five of the species of the southeastern United States have conspicuously reticulate leaves and short styles 0.8–2 mm. long. *Bumelia lanuginosa* (Michx.) Pers., of wide distribution (Florida to Missouri, Kansas, Texas, southern Arizona and northern Mexico), is a more or less thorny shrub or tree to 15 m. tall, with leaves loosely woolly-villous beneath and fruits 7–15 mm. long. Two of its three subspecies occur in our area: subsp. *lanuginosa* (*B. rufa* Raf.) with tawny pubescence, ranges almost entirely east of the Mississippi River, and subsp. *oblongifolia* (Nutt.) Cronq., with gray to almost white pubescence, almost entirely to the west. Subspecies *rigida* (Gray) Cronquist, with small leaves and a different altitudinal range occurs entirely to the west of our region. *Bumelia lycioides* (L.) Pers. (including var. *virginiana* Fern., *B. Smallii* Clark, *B. cassinifolia* Small, *B. lucida* Small), a shrub or small tree with leaves silvery strigose or sericeous beneath, but glabrate in age, and with fruits 7–13 mm. long, ranges from Florida north to southern Virginia, southern Indiana, southern Missouri and to Arkansas and eastern Texas. *Bumelia reclinata* (Michx.) Vent., with small leaves, hairy when young but soon glabrate, and with small fruits (4–7 mm. long), is restricted to Florida and southern Georgia. It consists of var. *reclinata* (including *B. microcarpa* Small), with whitish or grayish leaf-pubescence and sparsely hairy young twigs, and of var. *rufotomentosa* (Small) Cronq., with coarser, rufous leaf-pubescence and densely rufous-tomentose twigs, which is of local distribution from Alachua to Orange and Hillsborough counties, Florida. *Bumelia Thornei* Cronq., of Early, Baker, and Calhoun counties, Georgia, appears to combine the characters of *B. reclinata* and *B. lanuginosa*. *Bumelia tenax* (L.) Willd. (including *B. lacuum* Small, *B. megacocca* Small), a shrub or small tree with leaves densely sericeous or sericeous-tomentose beneath with tawny, rufous or white [f. *anomala* (Sarg.) Cronq.] hairs, is restricted to the Coastal Plain from South Carolina to Florida.

The sixth species, *Bumelia celastrina* HBK. (*B. angustifolia* Nutt.), is characterized by small, fascicled, inconspicuously reticulate leaves, by twigs, leaves, pedicels and sepals glabrous from the outset, by styles about 2.5–4 mm. long, and by fruits 7–13 mm. long. It occurs in the Bahamas, central Cuba, and southern Florida, northward along the coasts to Brevard and Levy counties, and from southern Texas southward through Central America to Venezuela.

Cronquist suggests that *Bumelia persimilis* Hemsl. (Mexico to Venezuela) is the most primitive species of the genus and that evolutionary trends are toward reduction in size of plant, in size of leaves and prominence of reticulation, in size of fruits, and sometimes in number of flowers in a cluster.

Bumelia differs from *Dipholis* primarily by the possession of endosperm. The presence or absence of endosperm (admittedly difficult to determine in herbarium specimens) apparently parallels natural groupings on other bases, so that the genera usually may be distinguished without resort to this character. In *Bumelia* the plants are commonly spiny or thorny, the lat-

eral appendages of the corolla-lobes wanting (although present in our species), the ovary usually hairy (or only occasionally glabrous), the young as well as the mature fruits broadly rounded to subtruncate or even retuse at the apex, and the cotyledons fleshy. In *Dipholis*, by contrast, the plants are unarmed, the lateral appendages of the corolla-lobes always present, the ovary nearly always glabrous, the fruits tapering abruptly into the style, the cotyledons thin. Preliminary studies of woods also appear to justify separation of the two genera (Record, 1939).

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4. **Chrysophyllum** Linnaeus, Sp. Pl. 1: 192. 1753; Gen. Pl. ed. 5. 88. 1754.

Evergreen shrubs or trees with alternate, short-petioled leaves, ours smooth, shining above, satiny beneath with lustrous golden to brown hairs, the secondary lateral veins parallel to the primary, and the long axes of the areolae more or less parallel to the lateral veins. Flowers few to many in axillary clusters, or occasionally solitary. Sepals 5, in ours not over 3 mm. long, broader than long, obtuse. Corolla not over 6 mm. long, campanulate-cylindric, the lobes 5[4–11], the tube about as long as the lobes. Stamens 5[–10], adnate to the corolla at or near the level of the sinuses, the anthers extrorse; staminodia none (or occasionally in individual flowers 1 or more irregularly developed in the corolla-sinuses). Ovary surmounted by a short, columnar style and a 5[–7–12]-lobed stigma; ovules attached laterally or basilaterally. Seeds 1, or sometimes several, the seed-scar 5 mm. or more in length, broadly elliptic to subcordate [or narrow or covering nearly the whole surface of the seed]; endosperm abundant. TYPE SPECIES: *Chrysophyllum Cainito* L. (The name from Greek, *chrysos*, gold, and *phyllon*, leaf, in reference to the hairs on the lower leaf-surfaces.) — GOLDEN-LEAF, SATIN-LEAF.

About 11 species in tropical North America, 30 in South America, 15 in tropical West Africa, and 25 in Australasia (16 in New Caledonia); a single species indigenous in subtropical Florida.

Chrysophyllum oliviforme L., satin-leaf, is an evergreen shrub or small tree with an upright plume-like crown of dark green, smooth and shining, ovate leaves, the under surfaces densely covered with lustrous, copper-colored hairs. The small, white flowers, produced irregularly throughout the year, are followed by olive-like dark purple one-seeded fruits. The hard, close-grained, light brown wood is sometimes used locally in cabinet-work. Varietas *oliviforme* ($2n = 52$), with leaves more than 5 cm. long and several to many flowers in a cluster, is occasional in thickets and coastal hammocks of southern peninsular Florida and the Keys, northward to Brevard and Lee counties, and is common in the Bahamas and the Greater Antilles. Varietas *picardae* (Urb.) Cronq., characterized by smaller leaves and fewer flowers per cluster, is known from a few collections from Hispaniola.

Chrysophyllum Cainito, the star apple ($2n = 26$), a handsome tree grown for its excellent fruit, is frequent in cultivation in southern Florida.

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5. **Pouteria** Aublet, Hist. Pl. Guiane Franç. 1: 85. *pl. 33*. 1775.

Trees or shrubs with alternate, occasionally subopposite leaves, the primary lateral veins strongly arcuate near the margin, scarcely crowded. Flowers solitary or generally several in axillary clusters. Sepals 4–6[–12], distinct, decussate when 4, otherwise imbricate, in ours 4–9 mm. long. Corolla white to yellow or green, subrotate to cylindric, 4–7(commonly 5 or 6)-lobed, the inner lobes sometimes larger than the outer, shorter than the tube, papillate or sericeous outside. Stamens epipetalous, attached at or near the level of the sinuses [or at the base of the corolla], sometimes abortive. Staminodia alternate with the corolla-lobes and sometimes apparently in the same series [sometimes petaloid, rarely absent]. Ovary hairy, [1–]5–8[–10]-loculed, the ovules laterally attached. Fruit commonly fleshy, [sometimes sclerotic,] 1–several-seeded. Seeds with a long and often broad lateral hilum (or sometimes nearly the whole surface more or less grown to the pericarp); embryo with thick cotyledons; endosperm a thin layer or lacking. (*Lucuma* Mol., sensu many authors.) TYPE SPECIES: *Pouteria guianensis* Aubl. (The name derived from *pourouma-pouteri*, the Carib vernacular name of the type species.)

A genus of about 150 species, the largest number in tropical America,

with a number of species in Africa and in Australasia (about 28 species); representatives of two species in subtropical Florida.

Pouteria dominigensis (Gaertn. f.) Baehni is a small tree to 10 m. tall, with oblanceolate to obovate or elliptic leaves, and with evidently pedicellate yellow or white flowers (6–16 mm. long) either solitary or borne few together in the leaf-axils. The yellow, fleshy, edible fruits are 3–6 cm. in thickness and bear one to several seeds. Varietas *dominigensis*, with leaves essentially glabrous (except when very young) is distributed in Hispaniola, Cuba, the Bahamas, and subtropical Florida (where it apparently is rare). Varietas *cuprea* (Urb. & Ekm.) Cronq., differing in strongly rufous-strigose and only tardily glabrate leaf surfaces, is confined to Hispaniola.

The eggfruit or canistel, *Pouteria campechiana* (HBK.) Baehni, long known as *Lucuma nervosa* A. DC., is native from southern Mexico to Panama. It occurs in the hammocks of the Florida Keys and also in Cuba, either in cultivation or perhaps as a recent escape. A tree which sometimes attains a height of 25 m., this species has elliptic to narrowly obovate, glabrous leaves, rounded to acuminate at the apex, up to 35 mm. long and 10 cm. wide, and borne on petioles up to 4 cm. long. The flowers are clustered in the axils on pedicels about 1 cm. long and the subglobose or pyriform fruits, up to 7 cm. in diameter, are yellow, green or brownish with yellow or orange pulp with the consistency of hard-boiled egg-yolk. The species shows variation in size and shape of leaves, size and number of flower parts, and size and texture of fruits. Some of the numerous segregates which have been proposed may represent geographical varieties, but the final evaluation of these should be preceded by extensive field study.

Pouteria belongs to a complex about which there is little agreement as to generic lines. As currently treated, the group includes such generic segregates as *Calocarpum* Pierre and *Oxythece* Miq., but excludes as separate genera the New World *Micropholis* Pierre and the predominantly Australasian *Planchonella* Pierre.

Aublet's *Pouteria* was based upon a mixture of two discordant elements, for the fruit described and figured with the other parts of the plant is that of a species of *Sloanea* (Elaeocarpaceae). (See Radlkofer.) Although the name might be regarded as a *nomen confusum*, Radlkofer, after reviewing the situation, re-established *Pouteria* for that part of the type belonging to the Sapotaceae. In the past *Lucuma* Mol. (1782) has been applied to the species here considered as *Pouteria*. However, three of the five species originally described by Molina generally are agreed not to be sapotaceous, and, although the identity of the others is uncertain, the description is such that these, too, may be excluded from the Sapotaceae.

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Subfam. MIMUSOPOIDEAE Lam

6. **Manilkara** Adanson, Fam. Pl. **2**: 166. 1763, nom. cons.[2]

Evergreen trees or shrubs with alternate, leathery leaves often approximate or clustered at the ends of the stout branchlets, the primary lateral veins generally parallel, nearly straight, not crowded. Flowers of our species on pendent pedicels, solitary or 2 or 3 together in the leaf-axils. Sepals biseriate, 3 + 3 [rarely 2 + 2 or 4 + 4], persistent, reflexed in age. Corolla white or yellow, glabrous, the lobes as many as the sepals, each with a pair of petaloid dorsal appendages or these obsolete by fusion with the lobes. Stamens as many as corolla lobes and opposite them, epipetalous, the anthers sagittate; staminodia of the same number as stamens and alternating with them, petaloid to fleshy (or almost obsolete). Style linear, exserted; stigma entire; ovary ovoid to depressed globose, pubescent, 6–14-locular (in ours 9–12- or 6-locular), the ovules lateral in attachment. Fruit ellipsoid, ovoid to depressed globose, fleshy, 1- or several-seeded, capped by the persistent style. Seed with a long, lateral hilum; embryo with thin cotyledons; endosperm abundant. (*Mimusops* sensu Sargent, Small and others, in respect to American species; including *Achras* L., *Sapota* Mill., nom. rejic.) TYPE SPECIES: *Manilkara Kauki* (L.) Dubard (*Mimusops Kauki* L.). (The name from Malabar, *manyl-kara*, as given by Rheede in *Hortus Malabaricus*, applied to a species of this genus.)

A genus of about 85 species in four subgenera, in the tropics of both hemispheres (about 30 in Africa, 25 in Australasia, and 30 in the Caribbean, Central America and South America); two species, one native, the other introduced, in subtropical Florida.

Manilkara bahamensis (Baker) Lam & Meeuse (*Achras emarginata* (L.) Little, *Minusops emarginata* (L.) Britton), wild dilly or wild sapodilla, of the Florida Keys and the Bahamas, is an evergreen shrub or small tree with bluish-green, coriaceous, elliptic, blunt or emarginate, petiolate leaves

[2] Both *Achras* L. and *Manilkara* Adans. have been proposed for conservation. (See Little, Brittonia **7**: 48, 49. 1949, and Lam and Van Royen, Taxon **2**: 112. 1953, respectively.) The former has been rejected (Taxon **3**: 119. 1954), while the latter has been approved by the Committee for Spermatophyta.

clustered at the ends of the stout branchlets. The small, yellowish flowers on recurved pedicels are borne singly or in two's or three's in the leaf-axils in April or May. The subglobose, fleshy, one-seeded, rusty-brown, mealy-roughened fruits reach 3 cm. or more in diameter. This taxon has been treated either as a species or, in the rather broad specific concept of Cronquist, as one of four subspecies of *Manilkara jaimiqui* (Wright) Dubard.

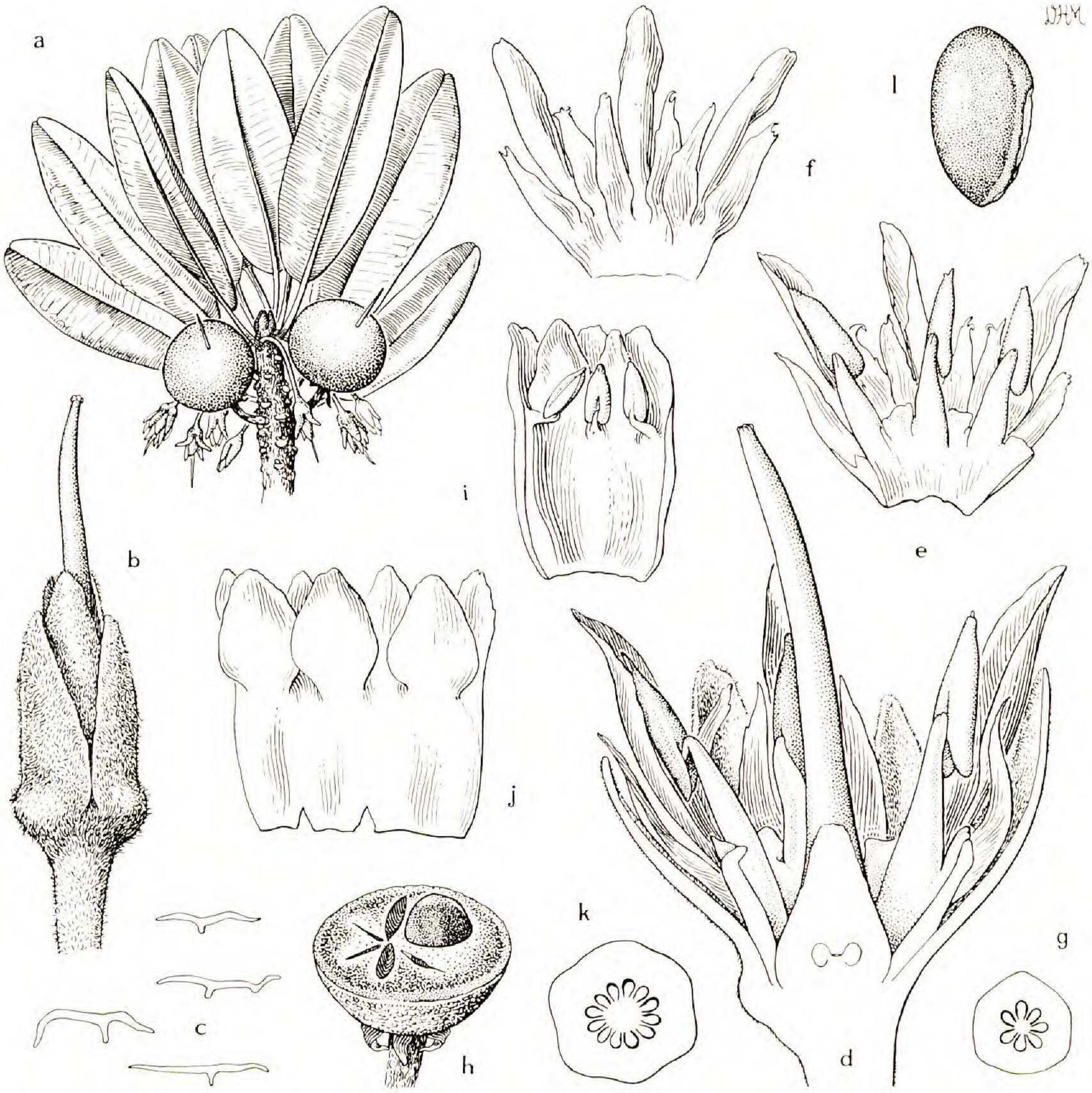

FIG. 2. **Manilkara.** a–h, *M. bahamensis*: a, tip of flowering and fruiting branch, × ½; b, flower, lateral view, after fall of corolla, × 3; c, detached two-armed hairs from calyx, point of attachment below, × 50; d, flower in vertical section, outer sepal to the left — note staminodia alternating with stamens, × 5; e, three corolla-lobes, from within, with appendages, stamens, alternating staminodia, × 3; f, three corolla-lobes, from without, to show dorsal appendages (cf. Fig. 1c, × 3; g, cross section of 7-locular ovary at level of attachment of ovules (semidiagrammatic), × 5; h, nearly mature fruit, the upper half removed, to show single seed, locules with aborted ovules, × 1. i–l, *M. Zapota*: i, portion of corolla, from within, to show three corolla-lobes, two petaloid staminodia alternate with stamens, × 3; j, portion of corolla, from without, to show three corolla-lobes, tips of four staminodia, × 3; k, cross section of 12-locular ovary at level of attachment of ovules (semidiagrammatic), × 5; l, seed, lateral view — note elongate seed-scar, × 1.

Our plant is subsp. *emarginata* (L.) Cronq.; the others are subspp. *jaimiqui* and *Wrightiana* (Pierre) Cronq., of Cuba, and subsp. *haitiensis* (Cronq.) Cronq., of Hispaniola.

Manilkara Zapota (L.) v. Royen (*M. Zapotilla* (Jacq.) Gilly, *Achras Zapota* L.), sapodilla, dilly, or naseberry, $2n = 26$, is cultivated in most of the warmer regions of the world for its excellent fruits. In its native area (Mexico to Costa Rica), especially in Yucatán, northern British Honduras, and Petén, Guatemala, it is also the principal source of chicle for chewing gum. The plant is a handsome evergreen tree with small, white flowers borne singly in the leaf-axils and followed by globose to ellipsoid fruits 3–9 cm. in diameter with translucent, pale brown flesh and several shining, black, compressed seeds. It is quite hardy in southern Florida, and outside of cultivation occurs in hammocks and old fields on the Everglade Keys and Florida Keys.

These two species would be placed respectively with *Manilkara* Adans. and *Achras* L., which, although similar in most respects, have been maintained as separate genera on the basis of the lack of paired dorsal appendages on the petals of the latter. However, the two genera were combined by Gilly who found transitional forms in his study of the *M. Zapota* complex. This union has been accepted generally, but the correct name for the genus so constituted has been a matter of controversy which is only settled by the conservation of *Manilkara* and the rejection of *Achras*.

A segregate of *Mimusops* L. (a group of about 60 species, mostly African), *Manilkara* is usually distinguished from that genus by sepal-number (6 *vs.* 8) and corresponding differences in the number of corolla-lobes, stamens and staminodia, by the seed-scars (relatively long and lateral *vs.* small and basilateral), by the nervation of the leaves (generally straight, parallel, and rather close *vs.* curved, wider apart), by the presence or absence of sclereids in the leaves (according to Lecomte — on the basis of only eight species), by the locules of the ovary (15–6 *vs.* 8), by the embryo (with thin, foliaceous *vs.* thick, plano-convex cotyledons), and by the presence or absence of endosperm. Although most workers at present recognize the two as distinct, a few species appear to be intermediate. On the basis of a preliminary study of Sapotaceous woods, Record thought that both might be included in a single genus.

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VENKATARAMAN, R., and F. J. REITHEL. Carbohydrates of the Sapotaceae. I. The origin of lactose in *A. Sapota*. Arch. Biochem. Biophys. **75**: 443–452. 1958.* [*Achras Zapota*.]

EBENACEAE (EBONY FAMILY)

Monoecious, dioecious, or polygamous trees or shrubs with alternate [rarely opposite], simple, entire, exstipulate leaves and watery sap; nodes with 1 trace from 1 gap. Flowers regular, 3–7-merous, sympetalous. Stamens epipetalous or hypogynous, 2–4 times as many as and opposite the lobes of the corolla. Gynoecium syncarpous, the styles wholly or partly distinct, the 2–16(–20)-locular ovary superior, with 1 (or 2) bitegumented ovules suspended from the summit of each locule. Fruit a berry. (Ebenaceae Vent. Tab. Regne Vég. **2**: 443. 1799, nom. cons. prop. [Type genus: *Diospyros* L. (*Ebenus* Burm. ex Ktze., not L.; *Maba* J. R. & G. Forster)]; Guaiacanae Juss. Gen. Pl. 155. 1789, nom. illegit. [Type genus: *Diospyros* L. (*Guaiacana* Tourn., not *Guaiacum* L.)].)[3]

A small, geologically old family, well represented in the fossil record, including four or five weakly defined genera (all except *Diospyros* confined to Africa or Madagascar) and about 450 living species, almost all restricted to tropical regions of both Eastern and Western hemispheres, with the greatest concentration of species in India and Malaysia, several in subtropical regions, a few species in the temperate regions of Asia and America, and none in the colder parts of either hemisphere.

The watery sap, usually unisexual flowers, and 2-integumented, pendulous ovules distinguish the Ebenaceae from the Sapotaceae which have milky sap, usually bisexual flowers, and 1-integumented, ascending ovules. The Styracaceae, with which the Ebenaceae are also thought to be allied, have bisexual flowers and an incompletely septate ovary (usually), which may be superior, half-inferior or inferior. Metcalfe and Chalk note a close general similarity between the woods of Sapotaceae and Ebenaceae, and Erdtman indicates that pollen grains more or less similar to those of Ebenaceae are found in the Sapotaceae and Styracaceae. The hairs of

[3] The well-known and long-used name Ebenaceae must be conserved, for it is derived not from that of a genus but from ebony, the wood of *Diospyros Ebenum*. (In establishing the family Ventenat wrote, "Les rapports que les plantes de cette famille ont avec l'arbre qui produit la véritable ébène, nous ont déterminés à leur donner le nom d'Ébénacées.") Linnaeus used *Ebenus* for a genus of Leguminosae, and the only post-Linnaean publication of the name in the sense of *Diospyros* (*Maba*) is that of Otto Kuntze, Rev. Gen. **2**: 408, 1891. Bullock (See Taxon **7**: 14, 17, 160. 1958; **8**: 170. 1959) has proposed conservation of Ebenaceae Vent. and rejection of Guaiacanae Juss. The former certainly must be conserved, but the latter is already illegitimate under the International Code of Botanical Nomenclature, being derived from *Guaiacana* Tourn. (not *Guaiacum* L., of the Zygophyllaceae), which does not seem to have been published as a generic name after 1754.

Ebenaceae are mostly unicellular, but are occasionally in tufts and sometimes are 2-armed.

The family is of economic importance for a number of woods, especially ebony, the hard and heavy, black heartwood of several Asiatic species of *Diospyros*, *D. Ebenum* Koenig being the classical source. Several species, mostly of *Diospyros* (see below), have edible fruits.

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1. **Diospyros** Linnaeus, Sp. Pl. **2**: 1057. 1753; Gen. Pl. ed. 5. 478. 1754.

Dioecious (or rarely polygamous) trees (or shrubs) with dense, hard wood. Flowers greenish, axillary, cymose, or the pistillate (larger than the staminate) solitary. Calyx [3]4–6[7]-lobed, accrescent in fruit, coriaceous or foliaceous. Corolla urceolate-campanulate with [3]4–6 lobes sinistrorsely contorted in the bud, spreading or recurved at anthesis, the tube usually contracted at the top. Stamens 3–many, usually in two or more rows, unequal, often in pairs, in ours mostly 16 in the staminate flowers (8 imperfect rudimentary ones in the pistillate or these sometimes absent), the filaments short, hairy [or glabrous], the anthers linear-lanceolate, arched inward, apiculate by the excurrent connective, 2-loculed, dehiscing laterally by longitudinal slits. Pollen 3-colporate. Styles usually 4, united below; stigmas emarginate or punctiform; ovary (rudimentary or absent in the staminate flowers) usually 8-locular [3 or 6, or 4 or 8–16-locular in other species], the ovules solitary [or 2] in each locule. Berry depressed-globose, globose, oblong or conical, sessile or subsessile, pruinose, bitter-astringent when green, orange, sweet, and soft-pulpy when ripe. Seed oblong, the testa brown, more or less shining, the endosperm cartilaginous, equable [or in some species ruminated by sinuous intrusions of the testa.] Embryo straight, the contiguous cotyledons foliaceous. Embryo sac development of the "Polygonum" type, seedless fruits sometimes developing. (Including *Maba* J. R. & G. Forster, *Brayodendron* Small.) TYPE SPECIES: *D. Lotus* L. (The name from Greek, *Dios*, of Zeus (genitive), and *pyros*, grain; used by Theophrastus for a fruit, adopted by Linnaeus in preference to *Guaiacana* Tourn., which was not of Greek or Latin derivation.) — PERSIMMON, DATE-PLUM.

A large genus of about 400 species of tropical and warm regions (including about 175 in Malaysia, 70 in Africa, 100 in Madagascar); only a few reaching into the temperate climates of North America and Asia; two species indigenous to the United States: *D. texana* Scheele, of southwestern Texas and northern Mexico (segregated on totally inadequate grounds as *Brayodendron* Small), and *D. virginiana* L., in the eastern United States.

Diospyros virginiana, persimmon, simmon, possumwood, a deciduous tree, usually 10–15 m. tall, with heavy, hard wood, ranges from Texas to Florida and northward to Connecticut and southeastern Iowa, but is uncommon in the area of the Wisconsin glaciation. Although the genus is known from the fossil record to have been distributed at one time far to the north, the present range of this species appears to be limited by temperature and rainfall, few specimens being found north of the 25° F. February isotherm or west of the 30-inch isohyet.

Phenotypically variable, *Diospyros virginiana* has received various taxonomic treatments and is in need of further study. Varietas *pubescens* (Pursh) Dippel (Florida to Arkansas, north to Virginia, southern Illinois, and southern Iowa) is characterized by villous or densely tomentose branchlets and leaves pubescent beneath. The form known as var. *platycarpa* Sarg. (Missouri, Arkansas, Kansas and Oklahoma) has broad, depressed fruits which ripen early, and var. *Mosieri* (Small) Sarg. (peninsular Florida) is said to be a shrub or small tree distinguished by thick-skinned, globose fruits and plump, slightly rugose seeds. Fruit-size and -shape are quite variable in this species and merit careful taxonomic attention. (See also references to *D. Kaki* below.)

The basic chromosome number of the genus appears to be 15, $2n$ having been reported as 30 for *Diospyros texana* and four exotic species (including *D. Lotus*), 60 (tetraploid) and 90 (hexaploid) for *D. virginiana*, and 90 for *D. Kaki* L. f. In *D. virginiana* the tetraploids occupy the central and southeastern parts of the range of the species, with the hexaploids on the periphery throughout. Morphological variation, as well as variation with respect to hardiness in this species, may be related to polyploidy. Sometimes used as a stock upon which *D. Kaki* is grafted, it provides ideal material for the study of stock–scion relationships with respect to ploidy.

Diospyros virginiana is self-pruning (as in species of *Salix*, *Populus*, *Ulmus* and *Quercus*), some of the twigs abscissing after the first year, most after the second, and some during successive years, while only relatively few are retained and become the stark, secondary branches of the tree. Root suckers are readily produced and clonal stands are frequent, especially in old fields.

Although the flowers are visited by bees in large numbers, the occasional development of seedless fruits (cf. *Diospyros Kaki*) has led to speculation concerning the necessity of fertilization for the production of the normal, seed-bearing fruits. There are, however, indications that pollination is necessary for ordinary fruit production and that fertilization does occur, although this latter process has not been observed.

Dormancy of the seeds is due, in part, to the mechanical resistance of the

seed coat, particularly the layer overlying the radicle. The physiological effects upon germination of the passage of the seeds through the alimentary tract of animals — such as foxes, deer, raccoons, and opossums — which feed upon the fruits, and the role of such animals in the spread of the species are not known.

A number of selections of *Diospyros virginiana* have been named, and the species is cultivated to a limited degree, although seldom on a commercial scale. Chinese and Japanese cultivars of *D. Kaki*, with large and delicious fruits, are cultivated commercially in northern Florida and California and are grown for ornament and fruit over much of our area. The numerous studies of *D. Kaki* suggest profitable lines of investigation on *D. virginiana*.

The closest relative of *Diospyros virginiana* appears to be *D. Lotus*, which, with *D. Kaki*, *D. Morrisoniana* Walp., *D. glaucifolia* Metc., *D. brideliifolia* Elmer, and, probably, *D. blepharophylla* Standl. (*D. ciliata* A. DC.), *D. ehretioides* G. Don, and *D. mollis* Steud. (according to Bakhuizen van den Brink), constitutes section DIOSPYROS (sect. *Lotus* Bakh.; sect. *Danzleria* (Bert.) Hiern, in part). The studies of the Malaysian species by Bakhuizen van den Brink and of the African by White have clarified many of the specific problems for those areas, but White has pointed out that the entire subgeneric classification needs a complete overhaul which must await careful study of all of the species. Among the African members White has noted well-marked, isolated species and a number of "superspecies" consisting of two to five closely related geographically or ecologically vicarious species. Standley, Bakhuizen van den Brink, and White have all found it impossible to maintain *Maba* as distinct from *Diospyros*.

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STYRACACEAE (STYRAX FAMILY) [4]

Shrubs or trees, usually more or less pubescent with stellate hairs [or peltate scales]. Leaves alternate, exstipulate, simple, entire, serrate or dentate, pinnately veined, the nodes with 1 trace from 1 gap. Flowers bisexual, in variously modified, basically cymose, terminal and axillary inflorescences (sometimes reduced to single axillary flowers). Calyx synsepalous, with 4 or 5 small teeth or lobes (or these obsolete), free from the ovary to completely adnate to it. Corolla sympetalous, usually 4- or 5-lobed [some-

[4] By C. E. Wood, Jr.

times more], valvate or imbricate in aestivation. Stamens usually twice (to 4 times) as many as the corolla lobes, inserted in a single series on the base of the corolla, the filaments usually more or less connate at the base, free above, usually continuous with the connective, the anthers oblong, 4-locular; pollen 3-colporate, usually suboblate. Gynoecium syncarpous, the ovary superior to inferior, (2)3–5-locular or 1-locular above by failure of union of the septa; style usually filiform; stigma terminal, usually minutely 3–5-lobed. Ovules 1–many in each locule, axile, anatropous, pendulous, or erect, 2-integumented, or 1-integumented (presumably by fusion of the two). Fruit typically dry, indehiscent or dehiscent; seeds 1 to several, the seed coat thin to indurate; embryo usually straight, with broad cotyledons, surrounded by fleshy endosperm.

A family of about 13 genera, all except *Styrax* small, including about 150 species, centering in eastern Asia, but with numerous species in the New World, none in Australia, one in the eastern Mediterranean region, and about three in Africa. The family exhibits the marked disjunctions indicative of an ancient group.

The Styracaceae are characterized by a series of characters which contrast markedly with those of the Symplocaceae (*q.v.*). They are distinguished from other sympetalous groups by the combination of watery sap; bisexual flowers with stamens at least twice as many as the petals and apparently in a single series; oblong to linear, basifixed anthers with longitudinal dehiscence; single, linear style; superior to inferior, 2–5-locular ovary; and usually dry, capsular to indehiscent fruit. Stellate pubescence is characteristic of the entire family, in contrast with the simple hairs of Symplocaceae, the two-armed hairs of Sapotaceae, and the several types found in the Ebenaceae. Erdtman notes that pollen more or less similar to that of Styracaceae is found in the Ebenaceae, and that at least slightly similar pollen occurs in the Cornaceae and Nyssaceae, while that of Symplocaceae is different.

The Styracaceae include a number of ornamental trees and shrubs (especially *Styrax* and *Halesia*). *Styrax officinale* formerly was the source of storax, a gummy resin used in incense, and from *S. Benzoin* is obtained benzoin, a resin which is secreted when the bark and wood of the tree are injured.

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1. **Styrax** Linnaeus, Sp. Pl. 1: 444. 1753; Gen. Pl. ed. 5. 203. 1754.

Deciduous [or evergreen] shrubs or trees with entire or slightly serrate or dentate leaves; nearly all parts more or less pubescent with stellate hairs (or rarely glabrous). Inflorescences terminal or axillary, basically cymose but appearing racemose, the axillary sometimes reduced to single flowers, as in *S. americanum*, thus giving the appearance of partly foliose racemes. Calyx synsepalous, cup-like, 5-toothed (or rarely 2- or 3-toothed) [or undulate or subentire]. Corolla 5 (rarely 6 or 7)-parted, always white, valvate, valvate-induplicate, or imbricate in aestivation, the tube (usually) much shorter than the lobes. Stamens 10 [8–18], adnate to the tube of the corolla in a ring [and monadelphous in a short tube], the filaments continuous with the connective, glabrous or pilose or densely pilose at the base. Gynoecium syncarpous; stigma small, minutely 3-lobed, terminal; style linear, with a canal; ovary partially adnate to the calyx [or rarely free], 3-locular at the base, 1-locular above (the 3 parietal septa united below but incompletely united above with the central placental mass); ovules axile, usually 4–6 in each locule, 2-integumented and with an obturator (a massive outgrowth of the placenta), one of the uppermost developing into a seed. Fruit globose or oblong, dry, loculicidally 3-valvate [or irregularly dehiscent or indehiscent]; seeds 1 or rarely 2, subglobose or ellipsoid, with a basilateral hilum, the testa hard, smooth [or crustaceous, wrinkled, papillate, or with stellate hairs]. TYPE SPECIES: *S. officinale* L. (The name Greek, *styrax*, the ancient name for storax, a fragrant resin formerly used in incense, and for the plant (*S. officinale*) from which it was obtained.[5] — STORAX.

A genus of about 120 species, mostly tropical and subtropical, of eastern Asia southward to New Guinea (but absent from the Philippines and Ceylon), the eastern Mediterranean region (a single species), South America, the West Indies, and Central America; about six species in the United States, two in our area. Two sections were recognized by Perkins: STYRAX (*Eustyrax* Perk.), with ovary 16–24-ovulate, and FOVEOLARIA (Ruiz & Pavon) Perk., with ovary 3–5 ovulate (2 species, Cuba and Peru).

Styrax americanum Lam., with flowers solitary or in pairs in the axils of leaves and paired at the tips of short branches, partially imbricate to valvate-induplicate aestivation of the corolla-lobes, and leaves 2–10 cm. long,

[5] Different authors have treated the genus as neuter, feminine, or masculine. *Styrax* is masculine in Latin. In Greek it is masculine, feminine, or neuter, depending upon its meaning: the spike at the lower end of a spear-shaft (m.), the shrub or tree from which storax was obtained (f.), or the resin storax (n.). Linnaeus took *Styrax* from the Greek (see "Critica Botanica") and treated it as neuter throughout his work. Although one would expect the word to be feminine, following the Greek gender for the plant, in this instance it should be argued that there was a choice. Under Recommendation 75A(1) of the International Code of Botanical Nomenclature, Linnaeus' consistent practice in this matter should be followed, whether or not he followed his own precepts.

is a frequent shrub of low, acid, mostly nonalluvial soils from southwestern Florida, northward on the Atlantic coastal plain to southeastern Virginia, into the mountains of northeastern Alabama, and in the Mississippi embayment to western Tennessee, western Kentucky, southern Illinois, Indiana and Ohio, southeastern Missouri, the southeastern half of Arkansas, and eastern Texas. Pubescence and seed- and fruit-size are variable within the species and should be studied in connection with the status of forma *pulverulentum* (Michx.) Perk. (var. *pulverulentum* (Michx.) Rehd.).

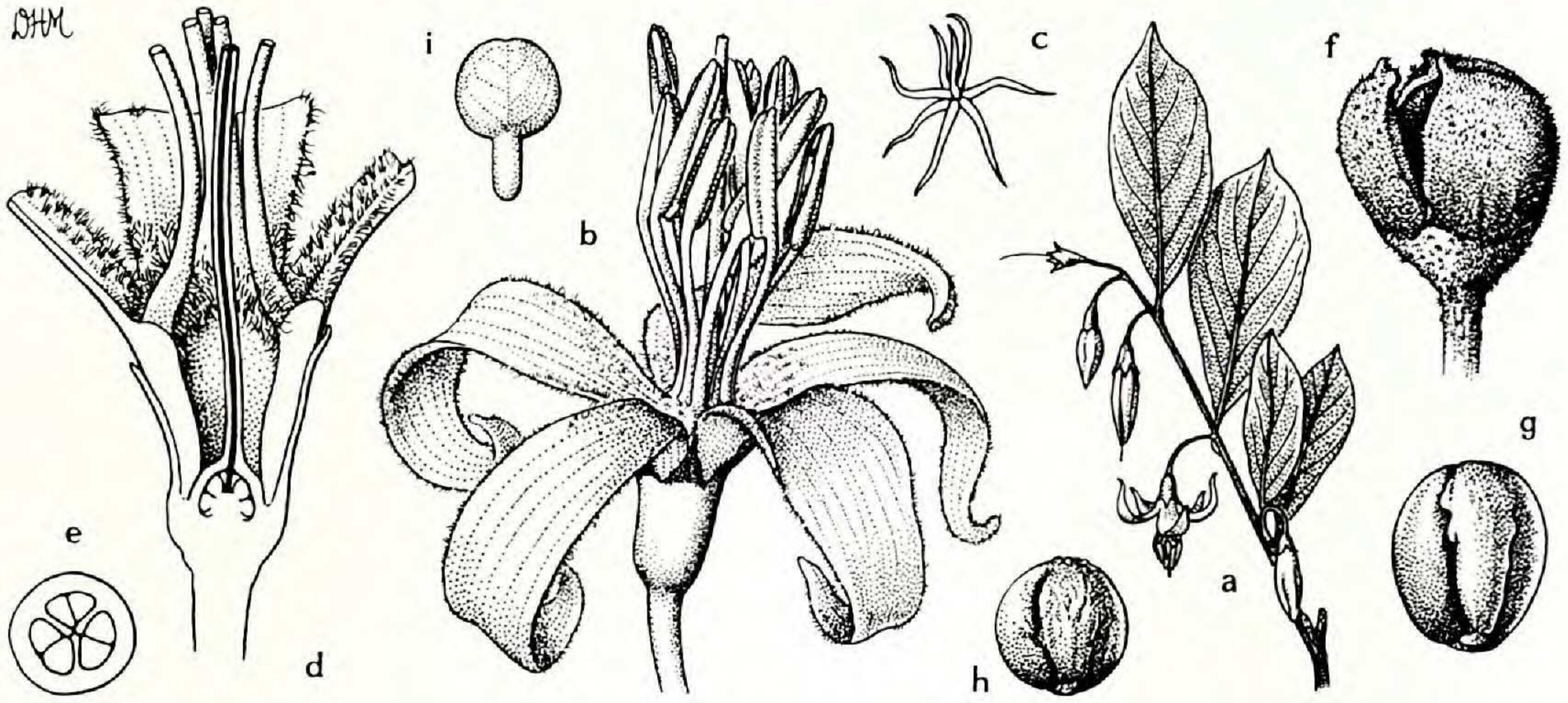

FIG. 3. **Styrax.** a–i, *S. americanum*: a, flowering twig, × ½; b, flower, × 3; c, stellate hair from petal, × 50; d, flower in vertical section, the distal portions of petals, stamens, and style removed — note partially inferior ovary, stylar canal, large placenta, incomplete septation, × 5; e, cross section of ovary through uppermost ovules to show incomplete septation (semidiagrammatic), × 8; f, capsular fruit with single large seed, × 2; g, h, seeds from two Florida collections — compare size, note prominent raphe and basal hilum, × 2; i, embryo, × 3.

Styrax grandifolium Ait., with larger, apparently terminal, mostly bracteate "racemes" (with as many as 20 flowers), imbricate aestivation, obovate leaves 5–20 cm. long, larger, somewhat more elongate fruits, and larger seeds, is a handsome shrub or small tree of woodlands, bluffs, and stream banks, ranging from northern Florida to Louisiana, northward to central Arkansas, northeastern Mississippi, western Tennessee (along the western edge of the Highland Rim), northern Alabama, northeastern Georgia, and through the piedmont and coastal plain of North Carolina to southern Virginia. Although the ranges overlap in large part, the two species seem to be completely isolated ecologically.

Section STYRAX was divided by Gürke and by Perkins into two series, *Valvatae* and *Imbricatae*, on the basis of aestivation of the corolla lobes. As Van Steenis has shown, however, imbrication may vary widely with respect to both the individual and species. (Cf. *S. americanum*.) Although both of our species were placed with the *Imbricatae* by Perkins, neither appears to be closely related to the other, and, with the exception of *S. glabrescens* Benth. (Hidalgo and Veracruz, Mexico, to Costa Rica), which

is close to *S. grandifolium*, the relatives of both are all species of eastern Asia. The chromosomes of *S. Obassia* Sieb. & Zucc. (related to *S. grandifolium*) have been reported as $2n = 16$, and those of *S. japonicum* Sieb. & Zucc. (close to *S. americanum*?) as $2n = 40$.

The embryology, morphology, and anatomy of *Styrax officinale* var. *californicum* (Torr.) Rehd. have been studied in some detail, and Van Steenis has pointed out numerous biological features of the species of the East Indies. Curious tubular galls of several characteristic shapes are produced on the Asiatic species by Aphidae of the genus *Astegopteryx*.

Six or more of the hardier species of *Styrax* are in cultivation in the United States for their showy white flowers.

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2. **Halesia** Ellis ex Linnaeus, Syst. Nat. ed. 10. 1044, 1369. 1759, nom. cons.

Deciduous shrubs or trees with membranaceous, serrulate leaves. Inflorescences reduced to clusters or irregular short racemes of 2–4(–5) long-pedicelled, pendent flowers in the axils of scars of leaves of the preceding year. Flowers 4-merous, showy, produced in early spring. Calyx almost completely adnate to the ovary, 4-ribbed, with 4 small teeth at the summit, or these obsolete. Corolla white to pale pink, campanulate, 4-cleft or -lobed, imbricate in aestivation but open long before anthesis. Stamens 8–16, united for about ⅓ their length and adnate to the lower part of the corolla; filaments straight, continuous with the connective; anthers oblong, slightly curved outward, introrse, dehiscing lengthwise. Style slender, linear, stigma minutely 4-lobed; ovary almost completely inferior, the sterile tip tapering into the style, 2- or 4-locular, each locule with four 1-integumented ovules attached near the middle of the axis, the 2 upper erect, the 2 lower pendulous. Ovary elongating greatly after anthesis; fruit dry, indehiscent, beaked and winged, with a hard, clavate-fusiform endocarp, a thin, corky mesocarp and 2 or 4 corky, longitudinal wings. Seeds 1–3, nearly cylindrical, against the wall of the endocarp, completely surrounded by a stony covering, the remaining cavity of the endocarp filled with corky tissue. (*Mohria* Britton, not Swartz; *Mohrodendron* Britton, *Carlomohria* Greene;

not *Halesia* P. Br., 1756, nom. rejic.) TYPE SPECIES: *H. carolina* L. (Named in honor of Stephen Hales, 1677–1761, author of "Vegetable Staticks" in 1722.) — SILVERBELL-TREE, SNOWDROP-TREE.

Two to four species of the southeastern United States and one species of Chekiang and Kwantung, China.

The genus is in need of a careful revision with particular emphasis on populations and studies of fully developed flowers and mature fruits. Herbarium materials are not very satisfactory in this group, for corollas and green fruits shrink and become distorted in drying, and the wings of ripe fruits are corky and brittle. In addition, the corolla attains its general shape early and is quite open while still green and half-grown, continuing to enlarge until (? or after) anthesis, thus leading to erroneous comparisons of size. Pubescence may be ephemeral, and plants may begin to flower at an early age.

Halesia diptera Ellis is a well-defined species distributed across the southern Coastal Plain in a band roughly delimited by Chatham County, Georgia; Leon County, Florida; Elmore and Chilton counties, Alabama; Ouachita and Natchitoches parishes, Louisiana; and Sabine and Harris counties, Texas. The type material came from near Augusta, Richmond County, Georgia, and the species has been reported in the Georgia piedmont in Meriwether and Upson counties. The plant is a shrub or tree up to 10 m. tall, with elliptic to obovate, abruptly long-acuminate, remotely sinuate-serrulate leaves, tomentose calyx and pedicels, a deeply cleft corolla 1.5–3 cm. long, with a very short tube and oval to obovate lobes, 8 equal stamens, 2-locular ovary (rarely 4-locular), and a fruit with 2 broad wings. Fruit shape is variable, with the wings either rounded or tapered at the base. Two varieties have been distinguished: var. *magniflora* Godfrey, described as limited to mixed woodlands of upland slopes, river bluffs, and ravine slopes in the limited area from Leon to Jackson County, Florida, with corollas 2–3 cm. long and lobes 1–1.5 cm. broad; and var. *diptera*, inhabiting flood-plain forests of the Escambia and Choctawahatchee rivers of western Florida, and ranging westward and northeastward, with corollas 1–1.5 cm. long and lobes 0.8–1 cm. broad. Further study is needed, for, although plants to the west of Florida appear to be small flowered, the larger-flowered plant apparently occurs in southwestern Georgia and adjacent Alabama, and, in Chatham County, Georgia, the easternmost locality for the species, the flowers are as large as those from Leon County, Florida.

A second group is the *Halesia carolina* complex which is distributed primarily from western North Carolina and eastern Tennessee to the coastal plain of Georgia, northern Florida, Alabama, and Mississippi. The group extends northward across western Virginia into southern West Virginia along the New River drainage, and scattered stations occur along the Cumberland River drainage (Harlan County, Kentucky; Davidson County, Tennessee), along the Tennessee River (Lauderdale County, Alabama; Hardin and Decatur counties, Tennessee), and on the Ohio River near the

FIG. 4. **Halesia.** a, b, *H. diptera*: a, fruiting branchlet, × ½; b, fruit variants, × ½. c–e, *H. carolina* var. *carolina*: c, d, flowering and fruiting branchlets, × ½; e, flower, lateral view, × 1. f–m, *H. carolina* var. *monticola*: f,

mouth of the Tennessee (Massac County, Illinois), suggesting migration along these routes by means of the floating, corky-winged fruit. An isolated series of stations occurs across central Arkansas into southeasternmost Oklahoma. Members of this complex have ovate to elliptic or oblong-obovate, acuminate, closely serrulate leaves; glabrous to tomentose pedicels and calyx; campanulate, shallowly lobed corollas 1–2.5 cm. long; 10–16 stamens; a 4-locular ovary; and 4-winged fruits 2–6 cm. long, with wings broad to narrow and rounded to long-tapering at the base. The extremes of the complex are distinctive, but the variation is puzzling and the taxa have not been carefully studied or clearly defined. One extreme, *H. monticola* (Rehd.) Sarg. (*H. carolina* var. *monticola* Rehd.), is a tree to 30 m. tall, of the higher mountains of North Carolina, Tennessee, and northern Georgia, with large corollas and large fruit with wings up to 15 mm. wide, truncate or rounded (and often widest) at the base. It appears to pass into *H. carolina* (*H. tetraptera* Ellis [6]), a shrub or tree to 10 m. tall, with

[6] Although *Halesia tetraptera* Ellis long has been identified with *H. carolina* L., the name recently has been adopted for *H. parviflora* Michx. on the basis of the illustration in Ellis' paper (Trans. Roy. Soc. London **51**: 931. *pl. 22*. 1761). From this illustration alone one may well conclude that the small flowers and tapering fruits illustrated are those of *H. parviflora* (described from St. Johns Co., Florida), but other evidence from the letters of Alexander Garden to John Ellis and from Ellis to Linnaeus (see J. E. Smith, A Selection of the Correspondence of Linnaeus, and Other Naturalists, from the Original Manuscripts **1**: 82, 83, 88, 92, 93, 373–382. 1821) suggests that the usual disposition of the name is the more correct one. From this correspondence it is clear that the plant was collected "on the hills, 200 miles to the northwest of that city [Charleston, S. C.] at a place called Saluda [Saluda Co., S. C.]," where Alexander Garden went in the course of June and July, 1755. In the spring of 1756, Garden's brother-in-law, a Mr. Perroneau, took to Ellis "the branch with the fruit, and a sprig with the flowers," which were the basis of the illustration by Ehret in Ellis' paper, along with mature fruits which, although planted in June, 1756, did not germinate until May of the following year.

Thus, although Ellis' published account of *Halesia tetraptera* (quoting from Garden) noted only that the plant "grows commonly along the banks of Santee river," the more precise information places the type locality off the Coastal Plain and apparently within the range of *H. carolina*, rather than that of *H. parviflora*. The seedlings raised in England by Ellis were almost certainly *H. carolina*, for as recently as 1951, both Bean (Trees and Shrubs Hardy in the British Isles. ed. 7. **2**: 80) and the Royal Horticultural Society Dictionary of Gardening fail to note *H. parviflora* in cultivation there, and the plant illustrated by Sims in 1806 (Bot. Mag. **23**: *pl. 910*), with the comment that this was first raised in England by Ellis from seeds sent over by Dr. Alexander Garden in 1756, can be only *H. carolina*.

Finally, Ehret's illustration in Ellis' paper, having been prepared from dried specimens sent by Garden, must be considered in terms of the shrinkage of flowers and fruits in drying and of the habit of the corollas of opening when only half grown. Both of these phenomena may apply here. The fruiting branch illustrated (see also reproduction of Ehret's illustration in Rhodora **60**: 86. *pl. 1231*. 1958) appears to represent *H. carolina* with the wings of the fruit somewhat shrunken in drying. The small flowering branch, on the other hand, bears flowers which appear to be not yet

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flower, lateral view, × 1; g, flower with two petals, eight stamens removed, × 3; h, ovary, vertical section, × 4; i, j, ovary, cross sections through lower and upper ovules, respectively, × 6; k, fruit, × ½; l, endocarp from a very large fruit, × 1; m, endocarp, cross section with seed, endosperm (stippled), embryo, and cavity, × 3; h–j, m, semidiagrammatic. n, *H. parviflora*: fruit, × ½.

smaller corollas and smaller fruit with narrower wings often tapering into the pedicel. The other extreme, *H. parviflora* Michx., a shrub or tree to 10 m. tall, perhaps restricted to sandy woods and bluffs of the Coastal Plain from Georgia and Florida to Mississippi, but possibly entering the Piedmont, has, in its best development, small, rather flaring corollas about 1.2 cm. long, pubescent calyces, and fruits 2.5–3.5 cm. long with narrow wings 3–5 mm. wide tapering into the pedicels (thus giving the effect of a clavate fruit). Most distinctive in northeastern Florida, this plant appears to intergrade with *H. carolina*; plants from the central areas of South Carolina, Georgia, and Alabama need special study in this respect. Throughout this complex the shape and size of the stony endocarp seem to be roughly the same; the varying shape and width of the four wings produces the wide range of fruit-shapes. The length of the style seems also to be more or less constant: thus it is equalled or exceeded by the corollas of *H. carolina* (including *H. monticola*), but protrudes from the short, rather flaring corollas of *H. parviflora*.

The Chinese species, *H. Macgregorii* Chun, combines a deeply parted corolla (as in *H. diptera*), four-winged fruits (as in *H. carolina*), and eight stamens of two lengths (eight equal stamens in *H. diptera*). The ovary is said to be 3-locular. *Halesia* (with *Nyssa*, *Carya*, and a few others) is of interest in being a genus of the eastern American–eastern Asiatic distribution in which more representatives occur in America than in Asia. In most genera following this pattern the Asiatic contingent appears both to be more numerous and to include more primitive species than the American. *Halesia* is most closely related to *Pterostyrax* Sieb. & Zucc., (5 species, Japan, China, Burma), *Rehderodendron* H. H. Hu (9 species, China, Indochina), *Sinojackia* H. H. Hu (3 species, China), and *Melliodendron* Hand.-Mazz. (2 species, China).

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at full size and which are perhaps somewhat shrunken in drying. The details of the corolla illustrated are hardly compatible with fully developed corollas of either *H. carolina* or *H. parviflora*. Fruiting material shrunken in such a way may be matched by *Fox 5265*, Rutherford Co., N. C. (GH); *Duncan 3349*, Clarke Co., Ga. (A); and *Faxon*, Oct. 1896, cultivated, Jamaica Plain, Mass. (GH). An instructive series is formed by *E. J. Palmer 20739*, *20763*, *26760* [*20760?*], April 11, 12, 1922, from near Page, LeFlore Co., Oklahoma (A): in these collections corollas of plants in various stages of development are approximately 2, 1.2–1.5, and 0.7 cm. long, respectively.

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SYMPLOCACEAE (SWEETLEAF FAMILY)

Trees or shrubs with alternate, simple, more or less coriaceous, exstipulate leaves, the nodes with one trace from one gap; complete, regular, sympetalous flowers; numerous[–4] stamens with ovate anthers; 2–5-locular inferior or half-inferior ovaries, typically with 2 pendulous, axile, 1-integumented ovules in each locule, and drupaceous or baccate fruits.

A small unigeneric family of approximately 300 species (placed in eight sections in four subgenera by Brand), of the warmer parts of America, Asia, and Australia (absent from Africa and Europe), the species very numerous in South America, about eight species ranging northward into Mexico, about 18 in the West Indies, and one in the United States, this primarily of our area, but extending into adjacent regions. Many of the species apparently are of local distribution, endemic to islands or mountains.

The Symplocaceae presumably are closely related to the Styracaceae, but differ in a number of characteristics: stamens usually in several series, often fasciculate (vs. stamens apparently in a single series in Styracaceae); ovate anthers (vs. oblong or linear anthers); inferior or half-inferior, completely loculed ovary (vs. superior to inferior, incompletely loculed ovary); baccate or drupaceous fruit (vs. dry, capsular to indehiscent fruit); simple hairs (vs. stellate or peltate hairs); usually rubiaceous stomata (vs. ranunculaceous stomata); solitary vessels with elongated pits between vessels and rays in the secondary wood (vs. solitary or clustered vessels with small, round pits between vessels and rays); and the occurrence of spiral thickenings in the vessels, commonly, and in the fibers, occasionally (vs. the lack of such thickenings).

The family is of limited economic importance. A few species are sometimes used for their wood, the leaves and bark of several (including *S. tinctoria*) yield a yellow dye, the roots of some are used in the preparation of tonics, and the leaves of several species are used as a substitute for *maté* (primarily from *Ilex* species). *Symplocos paniculata* (Thunb.) Miq.

(subg. HOPEA, sect. BOBUA), with terminal clusters of white flowers and methyl-blue fruits, and a few other Asiatic species are sometimes grown as ornamental shrubs.

The biological features of the group seem to have been studied hardly at all.

1. **Symplocos** Jacquin, Enum. Syst. Pl. Carib. 5. 1760; Select. Stirp. Am. Hist. 166. *pl. 175, fig. 68*. 1763.

Deciduous or tardily deciduous shrubs or trees with more or less coriaceous, sweet-tasting leaves. Flowers in congested or open, racemose or paniculate inflorescences, in ours about 6–14 in short, sessile, close clusters or racemes axillary to leaves or their scars, yellow, fragrant. Calyx adherent to the lower portion of the ovary, persistent, the 5 lobes valvate or imbricate. Corolla sympetalous, 3–11-lobed, deeply 5-lobed in ours, the tube short. Stamens [4–]many, conspicuous, exserted, in several unequal series, epipetalous at the base of the corolla, [free or monadelphous, the filaments connate in a tube, or] in ours pentadelphous, in 5 groups alternate with the corolla-lobes, the innate anthers short, orange, the filaments slender, white, distinct except at the base. Pollen usually 3-colpate. Gynoecium syncarpous; stigma terminal, slightly dilated or capitate, minutely lobed; style linear, the ovary inferior or half-inferior, in ours surrounded at the top by an orange-colored disc of nectariferous spongy tissue, 3[2–5]-locular; placentation axile, the anatropous (?)1-integumented ovules pendulous, typically 2 in each locule. Fruit drupaceous [or baccate], in ours cylindric-ellipsoid, about 1 cm. long; usually only a single seed developing; embryo straight [or curved], with short cotyledons, and with copious endosperm. (*Hopea* L. f., 1767, not Roxb., 1814.) TYPE SPECIES: *S. martinicensis* Jacq. (The name from Greek, *symplokos*, connected, twisted, entwined, apparently referring to the union of the stamens with each other and with the petals in *S. martinicensis*.)

Symplocos tinctoria (L.) L'Her., sweetleaf, horse-sugar, wild laurel, or yellow-wood, the only species indigenous to the United States, occurs from Sussex County, Delaware, southward to northern Florida and westward to eastern Texas and southeastern Oklahoma. Varietas *tinctoria*, with glabrous fruits, glabrous or glabrate current stems and tardily deciduous leaves, is widespread on the Coastal Plain, where it is largely restricted to hammocks, the margins of swamps and to sandy soils in association with *Pinus*, *Nyssa*, *Persea*, *Magnolia*, etc. Varietas *Ashei* Harbison, with pubescent fruits, persistently hairy stems, and promptly deciduous leaves, is distributed over a limited region of the southern Appalachians in western North and South Carolina, northern Georgia, and southeasternmost Tennessee (a single station in Polk County), between 1800 and 4500 feet in altitude, on dry ridges of chiefly acid, red-clay soils, where it is associated with *Pinus rigida* Mill., *Quercus coccinea* Muenchh., *Q. Prinus* L., and (formerly) *Castanea dentata* (Marsh.) Borkh. It appears largely to be lacking between mountains and Coastal Plain, although scattered sta-

tions may be expected in the Piedmont and are known from at least Aiken County, South Carolina, and Wake County, North Carolina. The geographical isolation of these varieties can be determined only after additional stations are sought, particularly in the Piedmont and in northern Alabama (where the species has been reported as far north as Marion, Cullman, and Morgan counties). Varietas *pygmaea* Fern., based upon dwarf, sterile specimens with small leaves, from white sands of dry pine barrens in Isle of Wight County, southeastern Virginia, is doubtfully distinct. The typical variety occurs in abundance in this general area of the state.

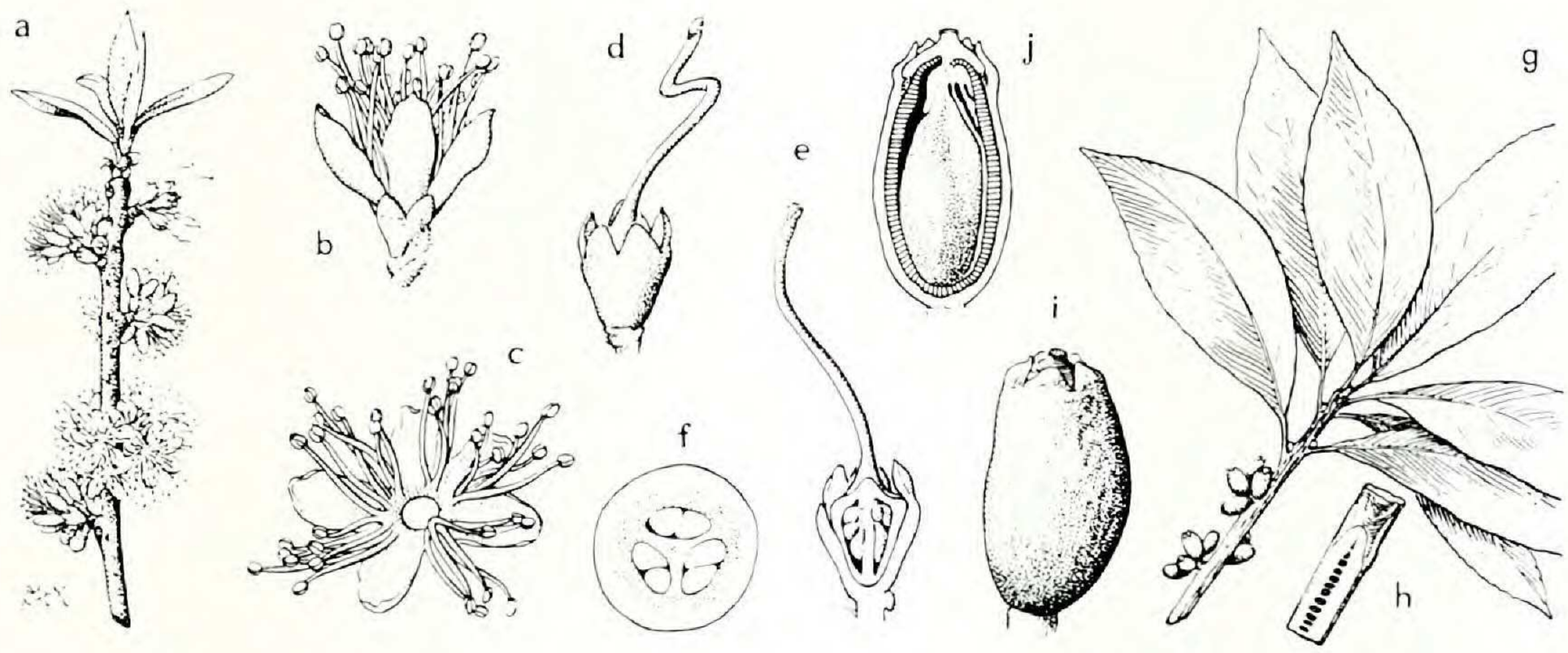

FIG. 5. **Symplocos.** a–j, *S. tinctoria* var. *tinctoria*: a, flowering twig, × ½; b, flower, × 2; c, detached corolla with stamens, × 2; d, flower with corolla removed, × 3; e, same, the ovary in vertical section (semidiagrammatic), × 3; f, cross section of ovary at anthesis — stippled area becomes sclerified in fruit (semidiagrammatic), × 6; g, fruiting twig, × ¼; h, portion of twig in oblique section to show diaphragmed pith, × ½; i, mature fruit, × 2; j, mature fruit, vertical section, the fertile locule with seed to left and center, abortive locules to right, × 2.

Characteristically a shrub, *Symplocos tinctoria* occasionally attains arborescent proportions (nearly 30 cm. in diameter and 12 m. tall) in the fertile river bottoms of Mississippi which usually are inundated for several weeks of the year.

Brand placed *Symplocos tinctoria* near *S. japonica* A. DC. and *S. setchuensis* Brand as the only American species of subg. HOPEA (L. f.) C. B. Clarke, sect. PALAEOSYMPLOCOS Brand, a group distinguished on the basis of the 3-locular ovary and clearly pentadelphous stamens with filiform filaments. However, because the summit of the ovary is glabrous and the united portion of the stamen-filaments is flattened (instead of round in section), Handel-Mazzetti and Peter-Stilbal excluded *S. tinctoria* from the subgenus (which was then renamed as subg. EOSYMPLOCOS), suggesting that its relationships should be sought among the New World species. Inconsistently, sections LODHRA and BOBUA (also of subg. HOPEA) were defined by the latter authors to include species with the apex of the ovary either glabrous or pubescent! It may be significant that at least some speci-

mens of *S. tinctoria* var. *Ashei* have a few hairs on the summit of the ovary at anthesis.

The subdivisions of *Symplocos* have been treated by some authors as separate genera, although most have maintained the group as a single genus with well-marked subgenera or sections. Erdtman, noting a variety of pollen types in *Symplocos*, suggests that pollen morphology "may be instrumental in subdividing the genus (or — if considered appropriate — in referring the different species to a number of genera now usually regarded as sections etc. under *Symplocos*)."

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